第50卷 第3期
2025 年3月

地球科学　Earth Science
http://www.earth-science.net

Vol. 50 No. 3
Mar. 2025

https://doi.org/10.3799/dqkx.2024.055

湖泊铁硫循环微生物研究进展

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摘　要: 湖泊作为内陆水体的重要组成部分,因将大气、岩石和水圈等联系起来而成为物质元素循环的关键作用场所.铁是地壳中含量排名第四的元素,普遍存在于各种矿物相中.硫以多种价态存在于多种无机和有机化合物中.湖泊中铁和硫在不同价态之间的相互转变和相互影响构成了湖泊铁硫循环过程,而微生物在其中发挥着主导作用,是循环中不可或缺的环节.本文总结了参与湖泊铁循环和硫循环的微生物类型、代谢途径及环境影响因子,特别聚焦于青藏高原湖泊铁硫循环相关微生物研究现状,并对未来青藏高原湖泊微生物驱动的铁硫循环研究方向进行了展望.

关键词: 湖泊;微生物;铁循环;硫循环;青藏高原.

中图分类号: P593　**文章编号:** 1000－2383(2025)03－887－21　**收稿日期:**2024－03－22

Research Progress on Microbes Involved in Lacustrine Iron/Sulfur Cycling

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Abstract: Lake, as an important part of inland water bodies, is a key site of action for the cycling of material elements by linking the atmosphere, rocks and hydrosphere. Iron, the fourth most abundant element in the Earth's crust, is prevalent in various mineral phases, and sulfur exists in various inorganic/organic compounds in a variety of valence states. The mutual transformation and interaction between iron and sulfur in different valence states in lakes constitute the process of iron and sulfur cycling in lakes, in which microorganisms play a dominant role and become an indispensable part of the cycle. This review summarizes the types of microorganisms, metabolic pathways and environmental influences involved in the iron and sulfur cycles in lakes, focusing on the current status of microbial research related to the iron and sulfur cycles in lakes on the Qinghai-Xizang Plateau, and presenting the future direction of microbial-driven iron and sulfur cycling research in lakes on the Qinghai-Xizang Plateau.

Key words: lakes; microorganisms; iron cycles; sulfur cycles; Qinghai-Xizang Plateau.

基金项目:国家自然科学基金重点项目(No. 42330410).

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引用格式:袁媛,刘勇勤,2025.湖泊铁硫循环微生物研究进展.地球科学,50(3):887－907.

Citation: Yuan Yuan, Liu Yongqin, 2025.Research Progress on Microbes Involved in Lacustrine Iron/Sulfur Cycling.*Earth Science*, 50(3): 887－907.

0　引言

湖泊生态系统作为陆地生态系统的重要组成部分，通过与地面的大气圈、岩石圈和水圈等联系在一起，从而成为各圈层相互作用的连接点．铁是地壳中丰富度第4的元素，在环境中主要以Fe^{2+}和Fe^{3+}价态存在于各种矿物相中，如氧化物（FeO、Fe_2O_3和Fe_3O_4）、氢氧化物（$Fe(OH)_2$和$Fe(OH)_3$）和碳酸盐（$FeCO_3 \cdot nH_2O$）等（Hedrich *et al.*，2011），其中三价铁氧化物是自然界中最主要的三价铁物种（Hansel *et al.*，2015a）．硫是氧族元素之一，在自然界中硫以从-2到$+6$的价态存在于各种化合物中，如黄铁矿（FeS_2）、石膏（$CaSO_4 \cdot 2H_2O$）等矿物相无机硫化合物，硫化氢（H_2S）、硫酸盐（SO_4^{2-}）等非矿物相无机硫化合物，硫醇（-SH）、硫醚（R-S-R）等有机硫化合物（Muyzer and Stams，2008）．

长久以来，铁循环被普遍认为是非生物介导的化学过程，即主要通过与分子氧（O_2）、亚硝酸盐（NO_2^-）、二价和四价锰（Mn）、各种各样的溶剂以及有机碳等发生化学作用进行循环，直到分离得到铁代谢微生物（Lovley and Phillips，1988a；Schoenberg *et al.*，1988），微生物在铁的地球化学循环过程中的作用才被逐渐接受（图1）．参与铁氧化过程的微生物主要有3种（Tong *et al.*，2023）：（1）微嗜氧Fe^{2+}氧化细菌；（2）光养Fe^{2+}氧化细菌（光能和Fe^{2+}为电子供体，碳酸氢盐为电子受体）；（3）硝酸盐还原Fe^{2+}氧化细菌：

（1）$4Fe^{2+} + 10H_2O + O_2 \rightarrow 4Fe(OH)_3 + 8H^+$；

（2）$4Fe^{2+} + HCO_3^- + 10H_2O \xrightarrow{hv} 4Fe(OH)_3 + 7H^+ + CH_2O$；

（3）$10Fe^{2+} + 2NO_3^- + 24H_2O \rightarrow 10Fe(OH)_3 + 18H^+ + N_2$.

参与铁还原过程的微生物主要有两种（Wang *et al.*，2016；Dede *et al.*，2022）：（1）异化铁还原细菌；（2）铁还原耦合氨氧化细菌：

（1）$Fe(OH)_3 + 3H^+ \rightarrow Fe^{2+} + 3H_2O$；

（2）$NH_4^+ + 6FeOOH + 10H^+ \rightarrow NO_2^- + 6Fe^{2+} + 10H_2O$.

自然界中参与硫循环的微生物包括2种（陈俊松等，2020）：硫氧化细菌（sulfur-oxidizing bacteria，简称SOB）和硫酸盐还原细菌（sulfate-reducing bacteria，简称SRB）．因硫化合物价态的多样性，硫氧化细菌参与的将低价态硫氧化为高价态硫的过程包括：硫化物或硫代硫酸盐氧化为单质硫，单质硫氧化为亚硫酸盐，亚硫酸盐氧化为硫酸盐（Wu *et al.*，2021）（图2）．相对应地，硫酸盐还原细菌是将高价态的硫酸盐还原为硫化物或硫单质，包括同化硫酸盐还原和异化硫酸盐还原，异化硫酸盐还原过程因会产生能量而普遍存在于自然环境中（Pereira *et al.*，2011）（图2）．

经典氧化还原电势表明，微生物还原Fe^{3+}能力高于硫酸盐（Flynn *et al.*，2014），并认为除在高硫酸盐环境下，普遍的硫酸盐还原对铁循环几乎没有影响，然而有研究表明，在硫酸盐含量较低的淡水沉积物中，硫酸盐还原是影响铁还原的主要因素，即硫化是铁还原的主要途径（Hansel *et al.*，2015a；Berg *et al.*，2019），这一观点将硫循环和铁循环连接起来，并表明硫循环中间体对铁循环的重要性．湖泊中铁和硫在不同价态之间的相互转变和相互影响，构成了湖泊铁硫循环过程（Holmkvist *et al.*，2011；Flynn *et al.*，2014；Lohmayer *et al.*，2014；Mills *et al.*，2016；Bao *et al.*，2017）．

铁硫元素在微生物驱动下的氧化还原过程同时会影响其他元素的循环，如碳、氮、磷等．光养

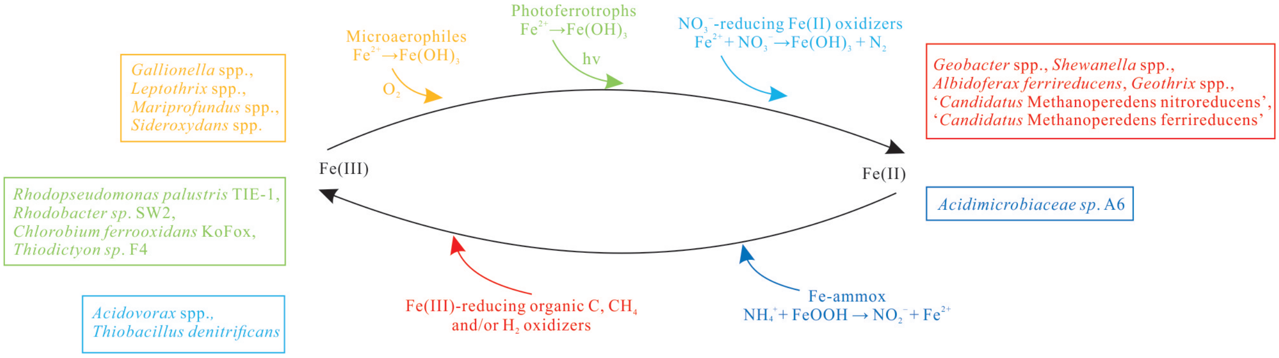

图1　微生物参与的铁循环

Fig.1　Microbially mediated iron cycle

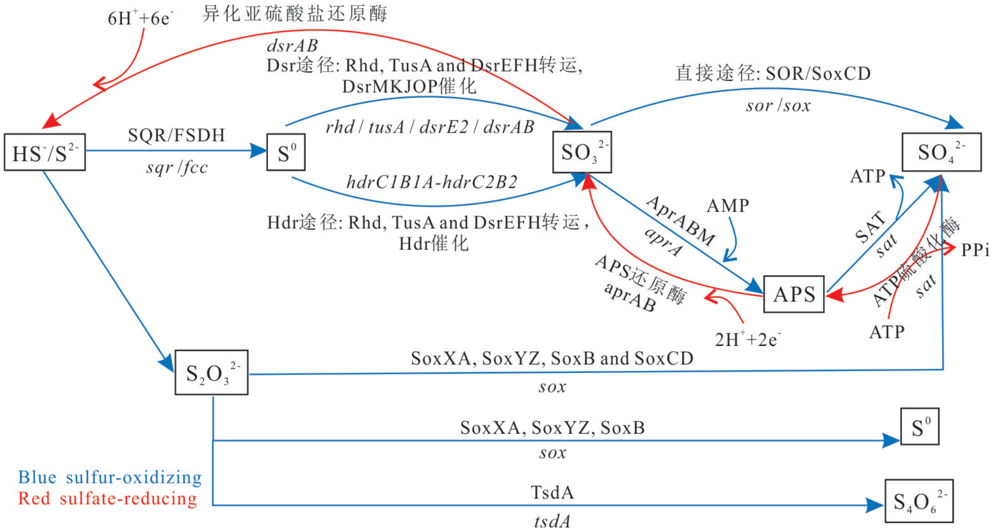

图 2　微生物参与的硫循环

Fig.2　Microbially mediated sulfur cycle

Fe^{2+}氧化细菌作为湖泊中的初级生产者之一,可利用光能和Fe^{2+}中的电子,将碳酸氢盐固定成有机碳(Widdel *et al.*, 1993).硫酸盐还原再矿化有机质、还原性硫化合物(如硫化氢、硫和硫代硫酸盐)作为光合作用的电子供体,均可以实现碳固定(Bryant and Frigaard, 2006).铁还原菌影响湖泊甲烷排放过程,其中铁还原细菌有 3 种方式抑制甲烷排放:第 1,铁还原菌通过与产甲烷菌竞争底物来抑制CH_4的排放, Karvinen *et al.* (2015)向湖泊沉积物中添加氧化铁,当氧化铁的含量大于 3% 时,50% 以上的CH_4排放被抑制;Fan *et al.*(2018)在分析富营养淡水沉积物的细菌丰度时发现,铁还原菌丰度和产甲烷菌丰度呈负相关关系.第 2,铁还原菌和甲烷氧化菌共同作用,通过促进甲烷氧化从而削减甲烷排放,如在典型富铁湖泊抚仙湖中,好氧甲烷氧化菌 *Methylomonas* 通过丙酮酸发酵途径将甲烷转化为乙酸等小分子有机物为铁还原菌提供碳源,铁还原菌通过胞外电子传递还原铁氧化物(Li *et al.*, 2023).第 3,一些产甲烷菌也具有铁还原过程,即利用乙酸或H_2还原铁氧化物,通过消耗产甲烷基质抑制甲烷生成(Bond and Lovley, 2002).此外,一些铁还原菌还能促进甲烷生成,Elul *et al.* (2021)对天然深层富铁沉积物宏基因组进行分析,结果表明铁还原菌发酵的最终产物之一——乙酸盐可作为产甲烷细菌或古菌的底物,从而促进甲烷生成.硫酸盐还原菌通过 2 种方式抑制甲烷排放:第 1,硫酸盐还原菌和产甲烷菌竞争底物,抑制CH_4排放(Liu *et al.*, 2018);第 2,硫酸盐还原菌与厌氧甲烷氧化古菌合作,以硫酸盐作为最终电子受体,将甲烷氧化为碳酸盐,降低甲烷的排放(Knittel and Boetius, 2009; Laso-Pérez *et al.*, 2023).此外,淡水湖泊中的Fe^{3+}还原耦合氨氧化过程,虽然可降低温室气体的排放,但也造成了氮损失.磷元素作为构成生物体的基本元素之一,在核酸合成和能量转移方面发挥着重要作用,但当磷元素在湖泊中含量过多时,就会造成水体富营养化,氢氧化铁可吸收磷导致其沉积在沉积物中,而铁还原菌对铁矿物的消耗会导致释放被吸附的磷(Mort *et al.*, 2010).

铁硫元素对其他金属元素循环也有重要影响,主要体现在 2 个方面:第 1 为生物作用,异化铁还原细菌除可以使用Fe^{3+}作为电子受体,也可以使用多种金属离子作为电子受体,如铬、汞、砷等,从而对金属元素循环产生影响(Pan and Giammar, 2020).第 2 为非生物作用(包含两种),异化铁还原细菌代谢产生的Fe^{2+}产物可作为还原剂,将环境中的其他金属还原,或铁氧化菌产生的各种铁矿物因为具有吸附性可以将金属元素固定在矿物相内(Gnanaprakasam *et al.*, 2017).

此外,铁硫元素氧化还原过程还极大地影响湖泊水质,其中铁还原菌和硫酸盐还原菌是湖水黑水团形成的关键微生物群(邢鹏等,2015; Yan *et al.*, 2022).在厌氧条件下,硫酸盐还原菌分解有机质生成H_2S、硫化物等还原性硫化合物,不仅具有一定臭味,还可与铁还原菌分解有机质生成的Fe^{2+}发生化学反应生成 FeS 等黑色沉淀物(Liang *et al.*, 2018; Cao *et al.*, 2020),这些黑臭物质

不断积累在湖泊上覆水中形成湖泊黑水团．Zhou *et al*.（2021）对比了黑水团产生前后沉积物中的细菌群落组成，结果表明黑水团产生的生物标志物大多与水生生态系统中的铁/硫循环相关．

湖泊中铁硫元素的形态主要受湖泊性质影响（杨文斌等，2016），沉积物中铁的分类依赖于不同的萃取方法（Chao and Zhou，1983；Patzner *et al*.，2020），一般包括Fe（Ⅱ）、碳酸盐铁、易提取铁氧化物、活性铁矿物等，不同顺序萃取方法获得的铁差别也较大（Raiswell and Canfield，1998）．Poulton and Canfield（2005）将铁划分为：碳酸盐结合态铁（菱铁矿、铁白云石）、易还原态铁（水铁矿、纤铁矿）、可还原态氧化铁（针铁矿、赤铁矿）、磁铁矿、低活性层状硅酸盐结合态铁、黄铁矿、非活性硅酸盐结合态铁．基于湖水化学组分进行分类，湖泊可分为碳酸盐型、硫酸盐型和氯化物型，其中硫酸盐型又可细分为硫酸钠型和硫酸镁型（郑绵平和刘喜方，2010），沉积物中无机硫主要包括S^{2-}、SO_3^{2-}、$S_2O_3^{2-}$、SO_4^{2-}、AVS、S^0、FeS_2等形态，酸挥发性硫化物（AVS）和二硫化物（FeS_2）是主要的硫存在形态，元素硫通常少量（＜总硫2%）存在于还原性沉积物中（Backlund *et al*.，2008）．

1　湖泊微生物参与的铁硫循环

1.1　铁氧化菌

将Fe（Ⅱ）氧化为Fe（Ⅲ），并在这一过程中获得能量的微生物被称为铁氧化菌（Fe（Ⅱ）-oxidizing microorganisms，简称FeOM）（Ilbert and Bonnefoy，2013）．铁氧化菌分布极为广泛，从淡水、海水、沼泽湿地等普通中性环境到酸性矿山废水、热液口等极端环境，从有氧到季节性缺氧再到永久缺氧环境等，微生物分类学表明铁氧化菌在古菌和细菌中均有分布（表1），例如细菌*Sideroxydans paludicola*、*Acidithiobacillus ferrooxidans*、*Rhodobacter capsulatus*等，古菌*Metallosphaera sedula*、*Sulfolobus metallicus*等（Emerson *et al*.，2010；Liu *et al*.，2019；Tan *et al*.，2019；Malik and Hedrich，2022）．根据铁氧化微生物的生存环境条件和代谢方式可分为4类：（1）嗜酸铁氧化菌（Acidophilic aerobic Fe（Ⅱ）-oxidizers），因所处环境pH通常低于4，所以微生物可以使用环境中能够稳定存在的Fe（Ⅱ）作为电子供体，以氧气、硫酸盐、硝酸盐等作为电子受体，*Acidithiobacillus ferrooxidans*是第一株分离纯化的嗜酸铁氧化菌，也是目前研究较为深入的铁氧化菌（Ehrlich，1963）．（2）中性微氧铁氧化菌（Neutrophilic microaerobic Fe（Ⅱ）-oxidizers）生存需要的氧气虽远低于大气中的含氧量，但仍能以Fe（Ⅱ）为电子供体，氧气为电子受体（王亚鑫等，2022）．（3）中性厌氧光合铁氧化菌（Anaerobic phototrophic Fe（Ⅱ）-oxidizers）进行不产氧光合作用，被认为是条带状含铁建造产生的原因（Han *et al*.，2020；Dreher *et al*.，2021），这类微生物包括紫色硫细菌（purple sulfur bacteria，简称PSB）、紫色非硫细菌（purple non-sulfur Bacteria，简称PNSB）和绿色硫细菌（green sulfur bacteria，简称GSB），分别属于Gamma-变形菌纲、Alpha-变形菌纲和绿菌门，分布的广泛性导致其代谢方式具有多样性，Fe（Ⅱ）、H_2或H_2S均可作为电子供体，有机碳或无机碳作为电子受体（Jones *et al*.，2015；Bryce *et al*.，2018a，2018b）．（4）厌氧硝酸盐还原铁氧化菌（Nitrate-reducing Fe（Ⅱ）-oxidizers）在氧化Fe（Ⅱ）的过程中会耦合硝酸盐的还原，Fe（Ⅱ）或有机物作为电子供体，硝酸盐作为电子受体（Carlson *et al*.，2013）．

Fe（Ⅲ）晶体氧化物可能会对细胞产生损伤，因此Fe（Ⅱ）氧化过程大都是在细胞外膜上完成，电子从细胞外膜到内膜上的传递由外膜细胞色素承担，其中铁氧化酶Cyc2在上述4类铁氧化菌中均有发现，表明微生物参与的铁氧化过程可以Cyc2作为生物标志（McAllister *et al*.，2019；Kappler *et al*.，2021）．对于不同类型的铁氧化菌，细胞外膜上排列的、参与电子传递的蛋白质有所差异，但总体的电子传递路径有两条，顺氧化还原电位流动和逆氧化还原电位流动，前者将电子传递给电子受体，后者将电子传递至NADH脱氢酶以产生NADH，以好氧铁氧化菌*Acidithiobacillus ferrooxidans*为例，顺氧化还原电位电子传递过程如下：Fe（Ⅱ）→Cyc2→Rusticyanin→Cyc1→Cyt aa3→O_2，逆氧化还原电位电子传递过程如下：Fe（Ⅱ）→Cyc2→Rusticyanin→Cyc A1→bc1→NADH脱氢酶→NADH（Ilbert and Bonnefoy，2013；Malik and Hedrich，2022）．

1.2　铁还原菌

微生物降解有机质释放电子，并将Fe（Ⅲ）作为末端电子受体，从而使得Fe（Ⅲ）还原为Fe（Ⅱ），能完成上述过程的微生物称为异化铁还原菌（Fe（III）-reducing microorganisms，简称FeRM）（Lovley *et al*.，1993）．异化铁还原菌存在于各种厌氧环境中，

表 1　铁氧化还原相关微生物

Table 1　Microorganisms related to iron redox

种属	分离地	类型	参考文献
Acidithiobacillus ferrooxidans	水圈	FeOB	Ehrlich, 1963
Acidimicrobiaceae sp. A6	水圈	FeOB	Huang and Jaffé, 2018
Acidimicrobium sp.	水圈	FeOB	Arroyo *et al.*, 2015
Sideroxydans paludicola	水圈	FeOB	Lin *et al.*, 2012
Metallosphaera sp.	水圈	FeOB	Kozubal *et al.*, 2008
Stenotrophomonas maltophilia	水圈	FeOB	Arroyo *et al.*, 2015
Dechlorospirillum sp. strain M1	水圈	FeOB	Picardal *et al.*, 2011
Alicyclobacillus ssp.	露天煤矿	FeOB	Kinnunen *et al.*, 2003
Leptospirillum sp.	搅拌罐	FeOB	Okibe *et al.*, 2003
Sulfobacillus sp.	搅拌罐	FeOB	Okibe *et al.*, 2003
Geobacter metallireducens GS-15	水圈	FeRM	Lovley *et al.*, 1987
Shewanella oneidensis	水圈	FeRM	Myers and Nealson, 1988
Bacillus sp.	水圈	FeRM	Pollock *et al.*, 2007
Pyrobaculum ferrireducens sp. nov.	水圈	FeRM	Slobodkina *et al.*, 2015
Thermococcus indicus sp. nov.	水圈	FeRM	Lim *et al.*, 2020
Alkaliphilus metalliredigens sp. nov.	水圈	FeRM	Ye *et al.*, 2004
Clostridium butyricum	微生物燃料电池	FeRM	Park *et al.*, 2001
Rhizomicrobium electricum	微生物燃料电池	FeRM	Kodama and Watanabe, 2011
Pseudomonas stutzeri	搅拌罐	FeRM	Wang *et al.*, 2014
Pseudomonas azotoformans	油污泥	FeRM	Nair *et al.*, 2007

海洋热液、湖泊沉积物、水稻土壤、热泉沉积物等环境均有已分离纯化的纯培养物(Lovley *et al.*, 1993; Wang *et al.*, 2009; Zeng *et al.*, 2015; Kato *et al.*, 2019),对这些纯培养物进行系统分类鉴定,结果显示异化铁还原菌在古菌、细菌和真菌中均有分布(表 1),例如古菌 *Pyrobaculum* sp.、*Thermococcus* sp. 和 *Acidiplasma* sp. 等,细菌 *Thermincola* sp.、*Sulfobacillus* sp.、*Bacillus* sp. 和 *Desulfitobacterium* sp. 等(Zavarzina *et al.*, 2007; Johnson *et al.*, 2008; Kunapuli *et al.*, 2010; Wrighton *et al.*, 2011; Esther *et al.*, 2015),真菌 *Meruliporia incrassate*、*Gloeophyllum trabeum* 等(Hastrup *et al.*, 2013).异化铁还原菌根据代谢过程可分为两类,呼吸型异化铁还原菌(respirative dissimilatory Fe(Ⅲ)-reducing microorganisms)和发酵型异化铁还原菌(fermentative dissimilatory Fe(Ⅲ)-reducing microorganisms)(Lovley *et al.*, 2004).呼吸型异化铁还原菌将降解有机质产生的能量全部用于自身细胞的代谢,并以模式菌地杆菌属 *Geobacter* 和希瓦氏菌属 *Shewanella* 的研究最为深入,前者为严格的厌氧菌,有机质被最终代谢为二氧化碳和水,后者为兼性厌氧菌,最终代谢产物是乙酸和水(Shi *et al.*, 2019a).发酵型异化铁还原菌仅将约 5% 的电子用于自身生长代谢,其余全部用于合成发酵产物,例如乙酸、乙醇、氢气等,代谢类型的多样性使得未有模式菌可代表这一类微生物(Luu and Ramsay, 2003;Kodama and Watanabe, 2011).

Geobacter 和 *Shewanella* 是深入研究异化铁还原菌的实验材料,以此为研究对象相关的异化铁还原机制有 4 种(图 3)(吴云当等,2016):(1)直接接触机制,微生物细胞膜上存在一系列按照一定顺序排列的细胞还原酶,它们从内到外接替完成电子的传递,并且存在于外膜上的细胞还原酶直接与不溶性的铁化合物接触,完成电子的传递,细胞外膜还原酶属于细胞色素 c 类蛋白,血红素 c 型的数量和辅酶因子的差异构成了多种细胞色素 c,例如 OmcA、MtrA、CymA 等(Breuer *et al.*, 2015).模式菌 *S. oneidensis* MR-1 已被证实细胞膜上存在一条完整的电子传递链,由多种细胞色素 c 类蛋白构成,由内至外电子传递方向为:CymA→MtrA→MtrB→OmcA/MtrC→Fe^{3+}(吴云当等,2016).(2)纳米导线,微生物能够自身分泌菌毛、鞭毛和绒毛等细胞附属物,这一结构不仅能极大地延长电子长距离传递,而且可以将电子传递至不溶性电子受体

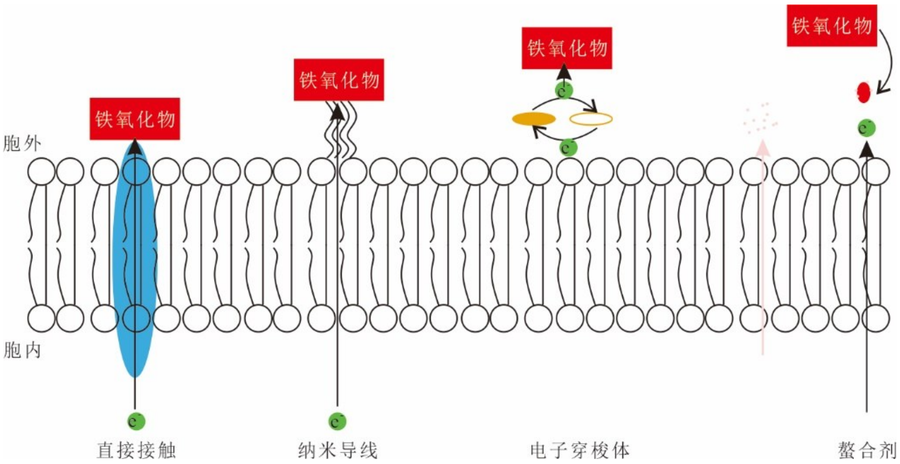

图 3　异化铁还原菌胞外电子传递机制

Fig.3　Mechanism of extracellular electron transport in heterogeneous iron-reducing bacteria

(Lovley *et al.*, 2012). *S. oneidensis* MR-1 在缺失 MtrC 和 OmcA 基因时，纳米导线是一种有效的将电子从细胞表面转移到氧化铁表面上的结构 (Reguera, 2018).(3)电子穿梭体，是微生物适应不溶性电子受体的另一策略，通过接受微生物释放的电子和传递电子给电子受体，电子穿梭体不断地在氧化态和还原态之间变换，从而完成电子的传递(马金莲等，2015). 核黄素(riboflavin)作为电子穿梭体发挥作用是由 von Canstein *et al.* (2008)首次在菌株 *S. oneidensis* MR-1 中确定，由于环境中存在难溶性 Fe(III)氧化物，菌株分泌核黄素将加速还原铁氧化物以促进自身生长.(4)螯合剂，通过改变电子受体在环境中的溶解状态，从而达到完成电子传递的目标 (Nevin and Lovley, 2002). 菌株 *Pseudomonas azotoformans* 可分泌铁载体，通过其与砷形成络合物，从而使砷的去除率提高近 60%(Nair *et al.*, 2007).

1.3　硫氧化菌

湖泊中微生物参与的无机硫氧化过程包括硫化物氧化、单质硫氧化、亚硫酸盐氧化和硫代硫酸盐氧化 4 个过程，即硫氧化菌(sulfur-oxidizing bacteria, 简称 SOB)将低价态的硫化合物氧化为高价态的硫化合物的过程. 目前研究较为深入的硫氧化菌类群为绿色硫细菌、紫色硫细菌、紫色非硫细菌和无色硫细菌(Ghosh and Dam, 2009)(表 2).(1)绿色硫细菌(green sulfur bacteria, 简称 GSB)属于厌氧菌，包括 *Chlorobaculum*、*Chlorobium*、*Chloroherpeton* 和 *Prosthecochloris* 等属(Sakurai *et al.*, 2010), GSB 虽然更偏向于氧化低价态的硫化氢和硫化物，但也可氧化硫单质，值得注意的是，GSB 区别于其他硫氧化菌之处在于，GSB 将氧化硫化氢和硫化物产生的硫单质留存在胞外(Gregersen *et al.*, 2011).(2)紫色硫细菌(purple sulfur bacteria, 简称 PSB)包括 *Chromatiaceae* 科和 *Ectothiorhodospiraceae* 科的菌株，PSB 主要以还原性硫化物或硫单质作为电子供体，多数 *Chromatiaceae* 科微生物将生成的硫单质贮藏在周质空间，*Ectothiorhodospiraceae* 科微生物则贮藏在胞外(Ghosh and Dam, 2009; Sander and Dahl, 2009).(3)紫色非硫细菌(purple nonsulfur bacteria, 简称 PNSB)主要包括 Alpha-变形菌纲中的 *Acetobacteraceae*、*Bradyrhizobiaceae*、*Hyphomicrobiaceae*、*Rhodobacteraceae* 和 *Rhodospirillaceae* 等科的菌株和 Beta-变形菌纲部分菌株，大多数 PNSB 通常在有氧的条件下氧化硫代硫酸盐，生成硫酸盐或连四硫酸盐，少数微生物的终产物是硫单质(Micciche *et al.*, 2020; Wang *et al.*, 2022b).(4)无色硫细菌(colorless sulfur bacteria, 简称 CSB)主要是指 Beta-变形菌纲、Gamma-变形菌纲、Epsilon-变形菌纲和少数 Alpha-变形菌纲的菌株 .CSB 因其不含光合色素而得名，与其氧化硫的类型、中间代谢产物的形成以及终产物的种类无关(Houghton *et al.*, 2016).

硫化物氧化的结果是产生硫单质，参与催化的酶是黄素细胞色素 c 硫化氢脱氢酶(flavocytochrome c sulfide dehydrogenase, 简称 FSDH)和硫化物醌还原酶(Sulfide: quinone reductase, 简称 SQR)，几乎所有的硫氧化菌都可完成这一过程 (Sousa *et al.*, 2018). 单质硫氧化为亚硫酸盐有 Dsr 和 Hdr 两条途径，前者由反向异化亚硫酸盐还原酶 (reverse dissimilatory sulfite reduction, 简称 rDsr)参

表2　硫氧化和硫酸盐还原相关微生物

Table 2　Microorganisms associated with sulfur oxidation and sulfate reduction

种属	分离地	类型	参考文献
Sulfolobus metallicus	水圈	SOB	Itoh *et al.*, 2020
Metallosphaera cuprina	水圈	SOB	Liu *et al.*, 2011
Chlorobaculum tepidum	水圈	SOB	Verté *et al.*, 2002
Rhodopseudomonas palustris	水圈	SOB	Brune, 1989
Thiobacillus thioparus	水圈	SOB	Sattley and Madigan, 2006
"*Candidatus* Sulfurovum sediminum" strain AR	水圈	SOB	Park *et al.*, 2012
"*Methylovirgula thiovorans*" strain HY1	水圈	SOB	Gwak *et al.*, 2022
Thiobacillus thiooxidans	土壤	SOB	Waksman, 1922
Mesorhizobium thiogangeticum sp. nov.	土壤	SOB	Ghosh and Roy, 2006
Fusarium solani	土壤	SOB	Li *et al.*, 2010
Desulfotomaculum thermocisternum	水圈	SRB	Nilsen *et al.*, 1996
Desulfovibrio paquesii	水圈	SRB	van Houten *et al.*, 2009
Desulfobulbus oligotrophicus	水圈	SRB	El Houari *et al.*, 2017
"*Candidatus Desulforudis audaxviator.*"	水圈	SRB	Panova *et al.*, 2021
Desulfobacter vibrioformis sp. nov.	水圈	SRB	Lien and Beeder, 1997
Desulfobulbus mediterraneus	水圈	SRB	Suzuki *et al.*, 2007
Desulfatiferula olefinivorans gen. nov., sp nov.	水圈	SRB	Cravo-Laureau *et al.*, 2007
Desulfosarcina variabilis	土壤	SRB	Wind *et al.*, 1999

与（Dahl, 2005），后者由类杂二硫化物还原酶（heterodisulide reductases-like, 简称Hdr）参与（Boughanemi *et al.*, 2016）．两种途径均需要Cys-SSH硫中继系统参与硫的运输，这一系统包括Rhd、TusA与DsrEFH三种转运蛋白（Dahl, 2015）．硫代硫酸盐可直接被氧化为硫酸盐或连四硫酸根离子，Sox酶复合体参与的硫代硫酸盐氧化生成硫酸盐的过程不产生亚硫酸盐，Sox酶复合体由*sox*基因簇编码合成，15个基因共编码合成4种关键蛋白，SoxXA、SoxYZ、SoxB和SoxCD；TsdA蛋白酶参与硫代硫酸盐氧化生成连四硫酸根离子，TsdA蛋白酶由*tsdA*基因编码（Rameez *et al.*, 2020）．亚硫酸盐到硫酸盐的氧化过程分为直接途径和间接途径，直接途径使用硫氧化还原酶（sulfur oxygenase/reductase, 简称SOR）或SoxCD蛋白完成失去两个电子的过程；间接途径分为两步，首先在AprABM复合体作用下亚硫酸盐与腺苷酸单磷酸（AMP）形成腺苷酰硫酸（APS），其次在腺苷磷酸硫酰酶（sulfate adenylate transferase, 简称Sat）作用催化下APS转化为硫酸盐，同时这一过程中会释放能量ATP，这对于环境中的微生物来说是有益的（Shi *et al.*, 2019b）．

1.4　硫还原菌

Beierinck于1895年发现一类微生物能将硫酸盐、硫代硫酸盐、亚硫酸盐等硫氧化合物还原为硫化物，同时会产生能量（ATP）用于微生物生长，这类微生物被称为硫酸盐还原菌（sulfate-reducing bacteria, 简称SRB；Bottrell and Newton, 2006）．SRB广泛分布于污水、土壤、海水、沉淀物等厌氧环境中（表2），微生物分类学将硫酸盐还原菌分为6大类（Daly *et al.*, 2000），脱硫肠菌属（*Desulfotomaculum*）、脱硫叶菌属（*Desulfobubus*）、脱硫杆菌属（*Desulfobacterium*）、脱硫细菌属（*Desulfobacter*）、脱硫球菌-脱硫线菌脱硫八叠菌属（*Desulfococcus-Desulfonema-Desulfosarcina*）和脱硫弧菌脱硫微菌属（*Desulfovibrio-Desulfomicrobium*）．

硫酸盐作为硫热力学稳定的氧化形式，不能直接被硫酸盐还原菌直接利用；因此，硫酸盐还原包括3个阶段（Muyzer and Stams, 2008）：（1）硫酸盐活化为腺嘌呤磷酰硫酸盐（adenosine 5′- phosphosulfate, 简称APS），该步骤需在硫酸腺苷转移酶存在的条件下，以消耗一个ATP为前提，使硫酸盐形成具有较强氧化状态的APS（Muyzer and Stams, 2008）；（2）APS被还原成亚硫酸盐，在APS还原酶的作用下，APS将进一步转化成亚硫酸盐和磷酸腺苷（Adenosine monophosphate, 简称AMP）（Broco *et al.*, 2005）；（3）亚硫酸盐被还原成硫化物，该步骤目前尚存在两种可能的解释机制，其一，亚硫酸盐通过连续失去三个双电子，生成连三硫酸盐和硫代

硫酸盐（$3SO_3^{2-}\rightarrow S_3O_6^{2-}\rightarrow S_2O_3^{2-}\rightarrow S^{2-}$），其二，亚硫酸盐直接失去六个电子（$SO_3^{2-}+6e^-\rightarrow 6H^+ + S^{2-}+3H_2O$）（Muyzer and Stams，2008）. 电子传递链是硫酸盐还原菌进行上述分解代谢过程中必不可少的组分，以 *Desulfovibrio* 为例，电子在其上的传递模式虽分为两种（Voordouw，2002），氢循环模型（Hydrogen cycling）和新模型（New model），但多种细胞色素 c 均在其中承担了重要角色（Aubert *et al.*，2000；Cypionka，2000）.

1.5　湖泊中微生物铁硫氧化还原过程

硫的生物地球化学循环以 3 个代谢过程最为重要，硫酸盐还原、硫化物氧化和硫歧化（Fike *et al.*，2015），但湖泊中硫循环的主动力是微生物介导的硫酸盐还原为硫化物的过程，期间会产生硫代硫酸盐、四硫酸盐、硫单质、亚硫酸盐等中间代谢产物（Hansel *et al.*，2015a）. 超过九成的硫酸盐还原形成的硫化物通常被再氧化回硫酸盐（Jørgensen *et al.*，2019）. 然而，一部分硫化氢可以被活性铁清除，产生硫化亚铁矿物，并最终产生黄铁矿埋藏在沉积物中（Berner，1984；Rickard and Luther，1997）.

湖泊中铁的快速循环，导致 Fe^{3+} 和 Fe^{2+} 变化不能被精准地测量，从而被称为神秘的循环（Boyd and Ellwood，2010），这种神秘的循环有两种产生的原因，第一种是非生物动力，Fe^{2+} 氧气或超氧化物氧化和 Fe^{3+} 氧化物光化学还原（Barbeau *et al.*，2001；Emmenegger *et al.*，2001；Sunda and Huntsman，2003；Boyd and Ellwood，2010），第二种是非生物和生物动力混合，非生物 Fe^{3+} 氧化物光化学还原和微生物介导的 Fe^{2+} 光氧化（Peng *et al.*，2019）. Berg *et al.*（2016）在永久分层的低铁含量 Cadagno 湖中观察到，光养 Fe^{2+} 氧化细菌贡献了 10% 的初级生产力，但未能检测到铁氧化物的存在，结合铁代谢微生物群落结果推测光是 Cadagno 湖铁循环的重要驱动力，可通过直接刺激光铁营养或刺激光合藻类的原位产氧，间接促进微需氧铁氧化以加强微生物铁循环. Peng *et al.*（2019）在实验室模拟厌氧 Fe^{2+} 光氧化微生物 *Rhodobacter ferrooxidans* SW2 的生长和铁循环过程，结果表明光化学还原 Fe^{3+} 产生的 Fe^{2+} 能被菌株 SW2 再次氧化，并将培养液中溶解性 Fe^{2+} 维持在较低的水平，但这并不影响菌株细胞的生长.

自然条件下，铁循环和硫循环长期被认为是相互独立、相互排斥的，且根据氧化剂的使用顺序，微生物对铁还原的作用是高于硫酸盐还原的（Lovley and Phillips，1987），然而，越来越多的研究揭示出硫元素对铁循环过程的影响，并证明了其在铁循环中的贡献. 在海洋沉积物中存在以硫参与的铁循环（Koretsky *et al.*，2003；Holmkvist *et al.*，2011），Kwon *et al.*（2014）在地下沉积物中发现硫酸盐还原菌产生的硫化物驱动的化学还原 Fe^{3+} 是沉积物中主要的铁还原过程. 在高硫酸盐系统中，微生物将硫酸盐作为末端电子受体是优先三价铁的，此外在淡水或陆地系统中，硫化物对铁循环几乎是没有影响的（Lovley and Phillips，1988b），然而 Hansel *et al.*（2015a）在含较低水平硫酸盐的池塘沉积物中发现，沉积物中铁还原过程与氧化铁是否易被微生物利用无关，而硫酸盐还原产生的硫化物才是铁还原过程的主导因素. 淡水沉积物中观察到 Fe^{3+} 氧化物的连续溶解和铁硫化物的产生，表明硫化物介导的化学铁还原成为主要的铁还原途径（Wu *et al.*，2019）. 此外，单菌铁/硫氧化还原过程中的电子转移途径也表明了硫元素对铁循环过程的影响，异化铁还原细菌 *S. oneidensis* MR-1 可以通过酶促还原 S^0 产生的硫化物非生物还原针铁矿，但不能直接还原针铁矿（Flynn *et al.*，2014）. 硫还原细菌 *Sulfurospirillum deleyianum* 将硫代硫酸盐酶促还原为硫化物，随后水铁矿的非生物还原与硫化物的再氧化相结合，从而间接完成还原水铁矿（Lohmayer *et al.*，2014）.

硫作为燃料参与到湖泊铁循环过程中在越来越多的环境中被证明（Mills *et al.*，2016），铁元素和硫元素之间的联系主要发生在铁还原和硫酸盐还原过程中，在厌氧环境下，硫酸盐还原生成的硫化物与铁氧化物发生纯化学反应，导致硫化亚铁沉淀，同时产生各种活性中间硫物种，如元素硫（S^0）、多硫化物（S_n^{2-}）或硫代硫酸盐（$S_2O_3^{2-}$）等（Kappler *et al.*，2021），这些中间体可以通过利用硫化合物的微生物（硫氧化菌和硫歧化菌）的活性再循环生成硫化物和硫酸盐（Berg *et al.*，2019）.

因此，湖泊中铁硫元素的循环过程不能独立进行分析，需要考虑二者的相互作用（图 4），此外，硫循环过程产生的各种中间代谢产物对铁循环的作用也需要被考虑到（Hansel *et al.*，2015b；Berg *et al.*，2019）.

1.6　湖泊铁硫氧化还原速率及影响因素

湖泊中微生物参与的铁硫氧化还原过程主要受所处水体环境的影响和制约，水体环境条件包括

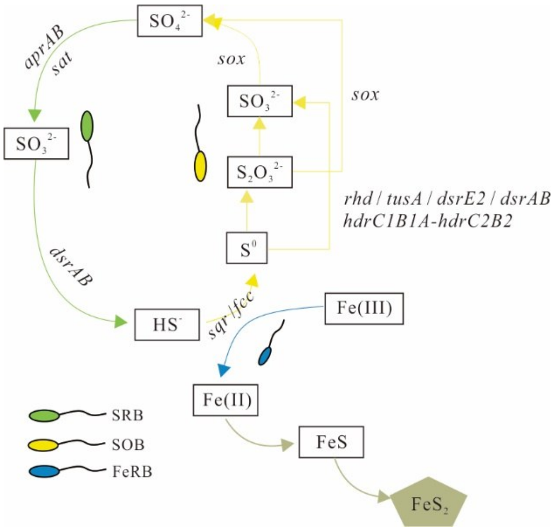

图4　湖泊中的铁硫相互影响

Fig.4　Iron-sulfur interactions in lakes

pH、营养物质、温度、氧气等理化因素以及各种铁硫形态等(Lovley, 1991; Aromokeye *et al.*, 2018; Han *et al.*, 2021).pH影响微生物的活性以及铁硫的存在形式(Hedrich *et al.*, 2011).碳、氮和磷等是水体环境中的营养物质，较高含量的有机质等营养物质将为微生物生长提供丰富的电子供体和能量来源(Yi *et al.*, 2013).

Fe(Ⅱ)在酸性环境中较为稳定，因此铁氧化菌受pH影响较大(Hedrich *et al.*, 2011).厌氧光合铁氧化菌仅在pH为6.5~7.0的范围内具有氧化Fe(Ⅱ)的能力，并且这类微生物的铁氧化能力也受到铁形态的限制，只能氧化溶解性亚铁，如硫化亚铁、菱铁矿等，而难溶的黄铁矿、磁铁矿等无法支持其生长(Kappler and Newman, 2004; Kappler, 2005).

富营养化区含有较高含量的有机质等营养物质，这不仅为铁还原菌提供了丰富的电子供体和能量来源，同时更容易产生缺氧环境，从而有利于*Geobacter*生长(Yi *et al.*, 2013).铁的形态是制约微生物铁还原能力的另一种因素，对于晶体Fe(III)氧化物，可溶性越高越容易被微生物还原，不同类型矿物相的铁氧化物被微生物还原从强到弱依次为水铁矿、纤铁矿、针铁矿、赤铁矿、四方纤铁矿、磁铁矿(曲东和Sylvia, 2001), Roden and Zachara (1996)的研究表明菌株*S. alga* BrY还原赤铁矿的速率仅是针铁矿的2%.

氧化还原条件直接影响湖泊中不同价态硫的空间分布，进而对塑造硫氧化群落结构产生影响(Kojima *et al.*, 2014)，硫化物具有较高的还原状态，因此氧化硫化物的SOB微生物通常在还原层湖水中丰度较高，如*Sulfurimonas*和*Sulfuricurvum*属(Pokorna and Zabranska, 2015).盐度影响微生物对渗透压的适应(Li *et al.*, 2022)，Nosalova *et al.* (2023)分析了两个不同盐度温泉的微生物硫氧化细菌的多样性，结果显示Epsilon-变形菌纲在高盐度的Stankovany泉水中很普遍，而Alpha-和Gamma-纲在低盐度的Jovsa泉水中很普遍.按照最适生长范围SOB可被分为嗜酸型、中性型和嗜碱型，相对应地，酸性湖泊中以嗜酸SOB为主要硫氧化菌类群，碱性湖泊中以嗜碱SOB为主要硫氧化菌类群(Sorokin and Kuenen, 2011; Rohwerder and Sand, 2007).

湖泊硫酸盐浓度是影响硫酸盐还原菌活性的因素之一，随着沉积物深度增加，硫酸盐浓度逐渐降低，从而使得硫酸盐还原菌代谢活力受到抑制(Kulp *et al.*, 2006).大多数硫酸盐还原菌是厌氧菌，因此氧气浓度也是影响硫酸盐还原菌活性的因素.不同硫酸盐还原菌能忍受的pH范围差异较大(1~9.8)，但大多数硫酸盐还原菌在pH为5~8时生长最旺盛(Yang *et al.*, 2021).底物供给细胞生长所需的能量，不同硫酸盐还原菌在利用底物进行代谢上也存在较大差异，如乙酸盐、乳酸盐等有机底物，或氢气等无机底物(Zeng *et al.*, 2019)，氮源对硫酸盐还原菌的生长维持和硫酸盐还原的有效性具有重要影响(Dev *et al.*, 2015).此外也有研究表明，腐殖酸类似物蒽醌-2,6-二磺酸盐(AQDS)可以选择性抑制硫酸盐还原菌，AQDS通过抢夺电子供体对硫酸盐还原菌产生抑制，抑制效果可使用光照得到增强；另外AQDS还在硫酸盐还原菌细胞中诱导了显著的膜去极化和超氧化物产生(Wang *et al.*, 2016).

2　青藏高原湖泊铁硫循环研究现状

2.1　青藏高原湖泊微生物

作为地球上海拔最高、面积最大的高原，青藏高原分布着数千个湖泊，它们拥有多个环境梯度特征(Jiang *et al.*, 2009)，如，大范围盐度梯度(0.1~426.3 g/L)，弱酸到碱的pH梯度(5.4~10.2)(Yang *et al.*, 2013b)，海拔从低于3 000 m到高于5 500 m梯度(Liu *et al.*, 2021).目前已完成超过80个湖泊的水质调查，包括湖水pH、溶解氧、溶解性有机碳、阴阳离子、总氮、总磷等理化指标(Liu *et al.*, 2021).

青藏高原湖泊微生物的研究，内容上包括湖泊微生物(细菌和古菌)群落组成和多样性调查、特定

代谢微生物类群在湖泊中的丰度调查和纯种微生物分离筛选等(Wang *et al.*, 2013; Yang *et al.*, 2013b; Xing *et al.*, 2021),研究手段上包括分子测序研究和细胞组分分析研究(Günther *et al.*, 2014; Deng *et al.*, 2017)等.环境因素对微生物群落结构的塑造具有重要作用,如盐度、季节、营养状况、地理距离等(Ji *et al.*, 2019; Zhao *et al.*, 2022),然而也有研究显示,小尺度的环境因素对群落结构的影响是重要的、确定的,如营养状态(Hansel *et al.*, 2015b),而大尺度的环境因素具有一定争议,如Wang *et al.* (2022a)认为海拔是影响青海高原3个邻近地区湖水中细菌组成、多样性最重要的因素,Wu *et al.* (2006)研究表明海拔对青藏高原东部海拔2 817～5 134 m的16个湖泊细菌群落组成没有显著影响.具有特定代谢类型的微生物类群在青藏高原湖泊的元素循环中扮演重要角色.一氧化碳氧化细菌可以将CO作为碳源,从而减少其向大气中的排放量(Yang *et al.*, 2013b),甲烷氧化菌参与湖泊甲烷氧化过程,对温室气体排放产生影响(Deng *et al.*, 2017).氨氧化是硝化作用的第一个限速步骤,是氮循环必不可少的过程,主要由氨氧化古/细菌完成(Hu *et al.*, 2010).Cheng *et al.* (2024)对青藏高原上6个水生态系统(咸水湖、淡水湖、河流、温泉、湿地和冰川)的498个宏基因组进行测序,构建了青藏高原微生物目录,并发现随着地理距离和海拔的增加,不同水生态系统中的微生物群落之间的相似性降低,且宏基因组之间的共享基因数量也减少,这可能是由于地理隔离和环境差异导致的微生物组成差异.

2.2　青藏高原湖泊铁硫循环微生物

青藏高原湖泊中微生物参与的铁循环研究较为有限,原因之一是因为微生物介导的铁循环过程缺少相应的标记功能基因,无法定量分析铁循环微生物的多样性.然而,Huang *et al.* (2022)仍通过将培养的最可能数(MPN)计数法与Illumina MiSeq测序相结合,分析了5种不同盐度(范围从0.67 g/L到346 g/L)的湖泊沉积物中富集的硝酸盐还原铁氧化微生物(Nitrate-reducing Fe(II)-oxidizing, 简称NRFeOx)的丰度和群落组成,结果表明盐度可能影响NRFeOx微生物的丰度、活性和营养模式.Fang *et al.* (2022)在宏基因组水平上的研究表明,铁的氧化可能会影响小柴旦湖沉积物中自养微生物的固碳途径.相比之下,硫循环微生物的研究较为深入,研究内容大致分为以下两个方面,(1)微生物种群丰度及多样性;(2)环境对微生物功能的影响.

Sox酶广泛存在于硫氧化微生物中,因而*soxB*基因(编码硫酸盐硫代水解酶)常被作为微生物参与硫氧化过程的标记功能基因,Yang *et al.* (2013a)对青藏高原4个湖泊的湖水和沉积物中硫氧化细菌种群的丰度和多样性进行分析,定量聚合酶链反应和基于*soxB*基因的系统发育分析结果显示,盐度在控制青藏高原湖泊SOB种群的多样性和分布方面起着关键作用.异化亚硫酸盐还原酶基因(*dsrAB*)作为分子标记,可用于对环境硫酸盐群落进行研究,Qin (2019)使用epicPCR技术来鉴定青藏高原盐湖沉积物中硫酸盐还原原核生物(SRP)的系统发育,在10个湖泊中共检测到883个SRP-OTU,并指出整个微生物群落的α-多样性与SRP群落的α-多样性呈显著正相关.

盐度是影响青藏高原湖泊微生物的重要因子之一,Huang *et al.* (2020)为模拟沉积物脱盐化后群落功能的改变,将茶卡湖(盐度299.3～350.7 g/L)的沉积物移植到盐度范围为0.3～299.3 g/L的不同湖泊中(Erhai Lake, Tuosu Lake, Gahai Lake2, Xiaochaidan Lake, and Chaka Lake),原位培养50 d后群落功能分析表明,脱盐过程会导致硫化合物呼吸、硫酸盐呼吸、硫呼吸、硫代硫酸盐呼吸、碳氢化合物降解、化能营养和发酵作用增强.Liu *et al.* (2022)使用宏基因组分析对盐度范围为0.7～31.5 g/L的青藏高原湖泊17个表层沉积物宏基因组进行分析,以预测硫循环相关基因的微生物功能的多样性和组成,结果表明,硫循环基因的Shannon多样性指数随着盐度的增加而降低,硫(异化硫还原和氧化、无机和有机硫转化之间的联系、硫歧化和还原)循环基因类别的相对丰度随着盐度的增加而降低,而硫同化硫酸盐还原和硫氧化基因类别显示出增加的趋势,硫循环基因的组成受盐度、总有机碳、总氮和总磷等环境因子的显著影响($p<0.05$),其中盐度的影响最大.Dong *et al.* (2006)对青海湖沉积物岩心的SSU rRNA基因进行测定分析,结果显示在深度为20 cm以下的样品中可能存在与各种硫酸盐还原菌序列高度相关的序列,但是在富集沉积物培养上未能培养出任何硫酸盐还原菌,结合沉积物缺乏硫酸盐和三价铁,认为青海湖沉积物中的主要代谢过程可能是生成甲烷.

3　青藏高原铁湖泊铁硫循环相关微生物分离研究

青藏高原半数以上的湖泊属于高盐度湖泊,是筛选嗜卤微生物的理想对象(Xu *et al.*, 2007; Wang *et al.*, 2013).然而对于与铁硫循环过程相关的纯培养微生物却少有分离株, Jiang *et al.*(2007)从茶卡盐湖沉积物岩心中分离得到 4 株与 *Shewanella putrefaciens* ACAM 576 和 *Shewanella baltica* W145 相似度在 99.2%~99.7% 的菌株,其中一株能够减少绿脱石中约 30% 的 Fe^{3+},该分离物还能够在有或没有 AQDS 的情况下,分别减少源沉积物(富含 Fe^{3+} 的粘土矿物中的结构 Fe^{3+})中 64% 或 42% 的 Fe^{3+}.

4　总结与展望

湖泊独特的栖息环境塑造了复杂各异的铁硫代谢微生物类群,它们互相协作、共同完成湖泊的铁硫循环过程,并对湖泊中其他的元素循环产生影响.本文主要综述了参与湖泊中铁硫循环的微生物代谢过程及其环境影响因子,调查了在青藏高原湖泊中微生物参与的铁硫循环相关研究进展.上述综述表明,铁氧化、铁还原、硫氧化和硫酸盐还原微生物的群落分布特征受到湖泊理化性质(如盐度、温度、氧气、有机质)影响,此外,对湖泊中铁硫循环过程的研究不能局限于微生物对单个元素循环过程的作用,多项研究结果表明硫酸盐还原作用对铁还原过程的贡献很大程度上高于铁还原菌.青藏高原湖泊地处高海拔、强紫外线、低温等极端气候条件,针对其微生物驱动的铁硫循环过程的研究可以进一步关注以下几个方面:(1)群落结构,研究不同类型青藏高原湖泊铁硫循环微生物的多样性和分布特征,以揭示不同湖泊中铁硫循环微生物的多样性和分布特征,这有助于理解高海拔湖泊中铁硫微生物群落对环境变化的响应;(2)功能活性,揭示青藏高原湖泊湖水和沉积物中微生物群落的铁硫氧化还原潜能,可以评估不同微生物在铁硫循环中的功能活性,为湖泊生态系统的生物地球化学循环提供基础数据;(3)影响因素,确定影响青藏高原湖泊铁硫循环过程的关键环境因子,这有助于预测气候变化等因素对湖泊生态系统的影响;(4)功能微生物,分离青藏高原湖泊中参与铁硫循环的微生物并揭示其代谢机制,这有助于发现新的功能微生物种类,深入理解湖泊生态系统中微生物的生态功能.以上研究的开展将有助于填补青藏高原湖泊铁硫循环过程研究的空白,提升对高海拔湖泊生态系统的理解,并为环境保护和可持续发展提供科学依据.

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